

FISH TRAILS IN THE UPPER CARBONIFEROUS OF SOUTH-WEST ENGLAND

by ROGER HIGGS

ABSTRACT. The ichnogenus *Undichna* Anderson, 1976, consisting of wavy horizontal grooves representing the drag marks of fish fins, is reported from the lacustrine Bude Formation. Two of the three species erected by Anderson are present. Two additional types of trail share strong similarities with Anderson's established species, but exhibit new features which warrant the erection of two new species, namely *U. britannica* and *U. consulca*. The new features necessitate modification of the original generic diagnosis.

U. consulca includes a broad, shallow furrow, suggesting that the fish swam with its belly brushing the sediment. This behaviour would have been impossible unless the pectoral fins were mounted abnormally high, to avoid fouling the sediment. Of four species of fossil fish previously known from the Bude Formation, one (*Cornuboniscus budensis* White, 1939) is remarkable for its high pectoral fins. It is suggested that the high fins were an evolutionary adaptation which enabled the fish to hug the bottom in search of food. This food may have included xiphosurid crabs, whose trackways (*Kouphichnium*) are intimately associated with the fish trails.

Of the four species of fossil fish found in the Bude Formation, two cannot be correlated with any of the trails; this suggests that the two species in question were mid- to surface-water feeders. None of the four known Bude fish species is morphologically suitable to have produced *U. britannica*, suggesting that a fifth species awaits discovery.

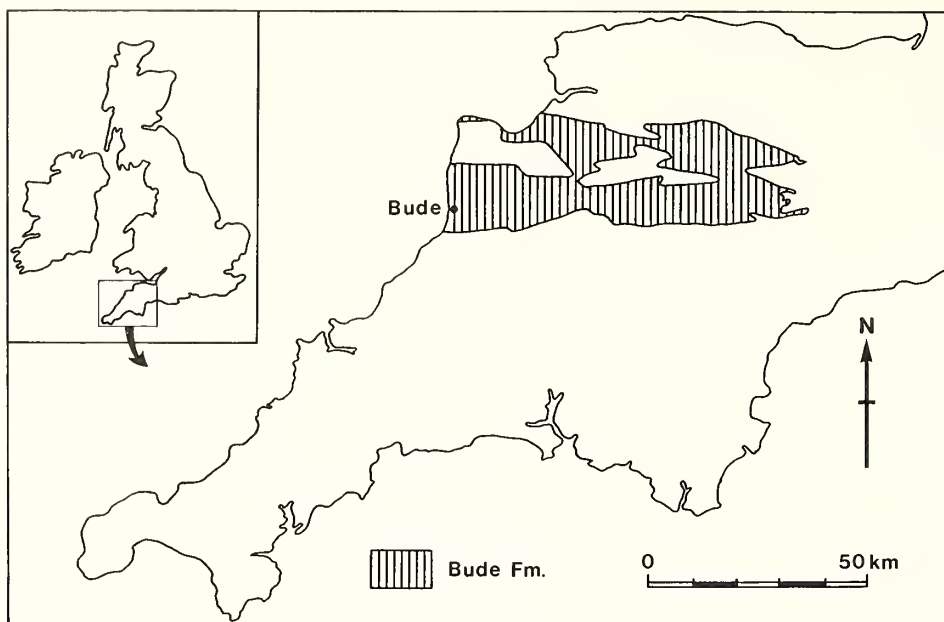
THE ichnogenus *Undichna* was proposed by Anderson (1976) for various combinations of sinusoidal and/or 'scolloped' waves; these were observed on parting surfaces in flaggy siltstones, and were interpreted as the drag marks of fish fins. Of the three species of *Undichna* erected by Anderson, two are reported here from the Bude Formation of south-west England (text-fig. 1). In addition, the Bude Formation has yielded two morphologically similar, but as yet unclassified, types of trace, for which two new ichnospecies are proposed.

All grid references (GR) given in this paper refer to Sheet SS of the UK National Grid.

GEOLOGICAL SETTING

The Bude Formation consists of about 1300 m of Westphalian A-C mudstones and sharp-based, very-fine sandstones (Higgs 1986a, b, and in prep.). Deposition is thought to have taken place on a broad shelf in an equatorial, foreland-basin lake, named 'Lake Bude' by Higgs (1986a). The sandstones are interpreted as turbidites, deposited by river-fed underflows during storm-floods; many show evidence for simultaneous wave action (Higgs 1986a). The shelf lay on the northern side of the lake, and passed southward into a flysch trough formed by thrust-loading in front of the N-advancing Variscan orogenic front. Unconformably overlying the Bude Formation are the post-orogenic continental deposits of the Stephanian-Triassic New Red Sandstone (Laming 1982). The Bude Formation is laterally equivalent to the (Lower and Middle) Coal Measures lying on the stable foreland immediately to the north, in central and northern Britain (Ramsbottom *et al.* 1978).

The Bude Formation shows a dm-m scale cyclicity, whereby two facies (F1 and F2) alternate. F1 consists of dark grey mudstone with sparse, thin (up to 20 cm) turbidites. F2 is coarser (shallower?) and consists of light grey silty mudstone/muddy siltstone with thicker (up to 40 cm) and often amalgamated (up to 10 m) turbidites. Body fossils, apart from three marine horizons (cm) with goniatites and pelagic bivalves, are limited to rare fish and crustacea in F1. *Undichna* has only been found in F2. Body fossils, trace fossils, and mudstone C/S ratios (Berner and Raiswell 1984) suggest



TEXT-FIG. 1. Map showing present-day outcrop of the Bude Formation (after Edmonds *et al.* 1975). Exposure is essentially limited to the coast, which is characterized by continuous cliffs and wave-cut platform.

that F1 and F2 were deposited in brackish water and fresh water, respectively (Higgs 1986*a, b*, and in prep.). The implied salinity fluctuations in Lake Bude can be explained in terms of a low-lying sill which was intermittently overtopped by sea water (cf. the Bosphorus (Scholten 1974)).

The supposed fish trails were first described by King (1965), who interpreted them as xiphosurid (king-crab) mating traces, as discussed below. The trails are exposed on parting surfaces in parallel-laminated (varved?) muddy siltstones (F2). This flaggy lithology is rare; the trails have only been observed at two stratigraphic levels, in each case in a 2–3 m muddy siltstone unit (King 1965). In both cases, *Undichna* is intimately associated with xiphosurid trackways (*Kouphichnium*; see King 1965, Goldring and Seilacher 1971, and Higgs 1986*b*); no other fossils are present in the units concerned.

The fact that fish trails and actual fish appear to be mutually exclusive (i.e. have only been found in F2 and F1, respectively) is probably an artifact resulting from (1) preferential *exposure* of fish trails in F2, due to the presence of flaggy lithologies, and (2) preferential *preservation* of fish in F1, due to anoxic bottom conditions (Higgs 1986*b*).

SYSTEMATIC PALAEOLOGY

The three species of *Undichna* erected by Anderson are all characterized by horizontal grooves in the form of waves with a regular wavelength. Two of these species are present in the Bude Formation. In addition, there are two other types of trace which are here assigned to the genus *Undichna* on the basis of regular wavy grooves; however, these traces are considered sufficiently different to justify the erection of two new species.

Location of specimens. All specimens mentioned in the paper are housed in the palaeontological collections of the University Museum, Oxford, except two specimens in the Geology Department of the University of Reading (UR14403 and UR14404).

Ichnogenus *UNDICHNA* Anderson, 1976

Diagnosis (emended). The genus includes those trace fossils comprising a set of horizontal waves (incised grooves) with a common wavelength and alignment. The waves may or may not be accompanied by a straight, continuous furrow, upon which they are superimposed. Individual waves may be continuous, or the troughs/crests may be preferentially absent or preferentially present. There may be as many as nine waves in a set; commonly, there are only two, and in some cases just one. Waves occur as (1) parallel pairs, (2) non-parallel pairs which are (a) intertwined or (b) separate, and (3) unpaired waves. These wave types occur in a variety of combinations. The traces are impressions (and corresponding moulds) on parting surfaces in flaggy lithologies.

Undichna bina Anderson, 1976

Text-fig. 2 (trail a)

Description. Only one specimen has been observed in the present study. The trail consists of a pair of sinuous grooves a constant distance (2.8 cm) apart. *U. bina* is the least complicated of the three species of *Undichna* erected by Anderson.

Interpretation. Anderson (1976) interpreted *U. bina* as the engravings of the pelvic fins (e.g. text-fig. 3) of a fish. The *pectoral* fins cannot be responsible: because they occur near the head, where the amplitude of undulation during swimming is practically zero (Bainbridge 1962), the pectoral fins would not leave a *sinuous* trail. The absence of waves attributable to the anal and caudal fins may be due to the 'undertrack fallout' effect described by Goldring and Seilacher (1971), whereby the 'copies' of a surface trace impressed through the surficial sediment become increasingly simple with depth due to the 'fallout' of less deeply impressed elements of the trace. Alternatively, these other fins may have been held clear of the sediment. In either case, the implication is that the pelvic fins protruded further below the body of the fish than all other appendages.

Undichna britannica nov. ichnosp.

Text-figs. 2 and 4

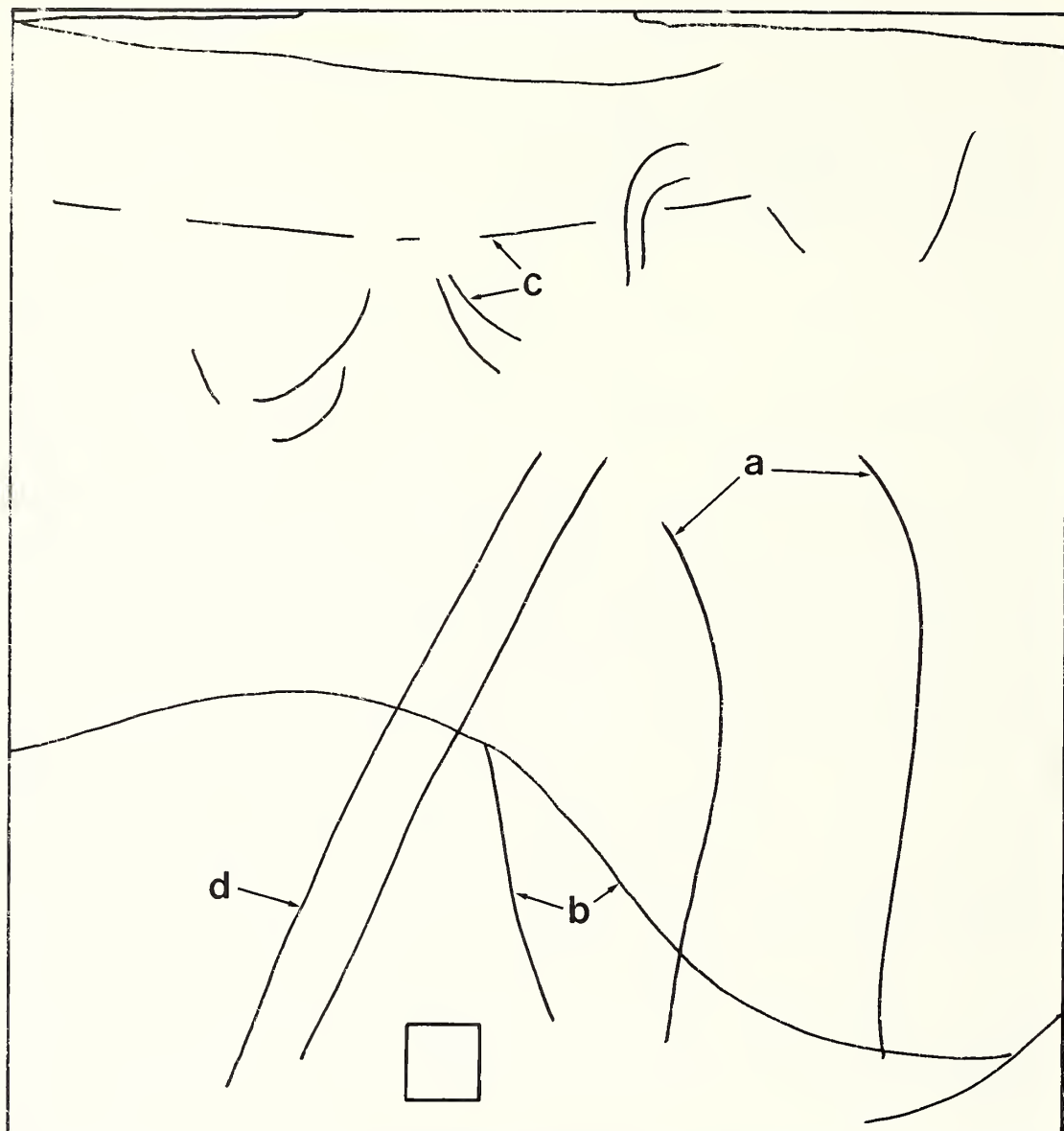
- 1965 undesignated xiphosurid 'nuptial embrace' trails, King, fig. 1.
- 1970 undesignated fish trail, Fliri *et al.*, fig. 9f.
- 1971 undesignated fish trails, Fliri *et al.*, fig. 8.
- 1976 ?*Undichna* sp., Anderson, pl. 54, fig. 5.
- 1984 *Undichna ?simplicitas*, Archer and Maples, fig. 7E.

Types. Holotype: specimen E.3841b, from a 2 m flaggy siltstone unit at the base of the cliff at GR (2017 0751), near Bude, Cornwall. Paratype: E.3842a, same horizon and locality as holotype. The siltstone unit occurs 4 m stratigraphically below a prominent 'marker shale' (F1), 5 m thick, known as the Saturday's Pit Shale (Freshney *et al.* 1979).

Diagnosis. The trace consists of a pair of sharply incised, intertwined grooves, each groove having the form of a sinusoidal or slightly asymmetrical sinusoidal wave.

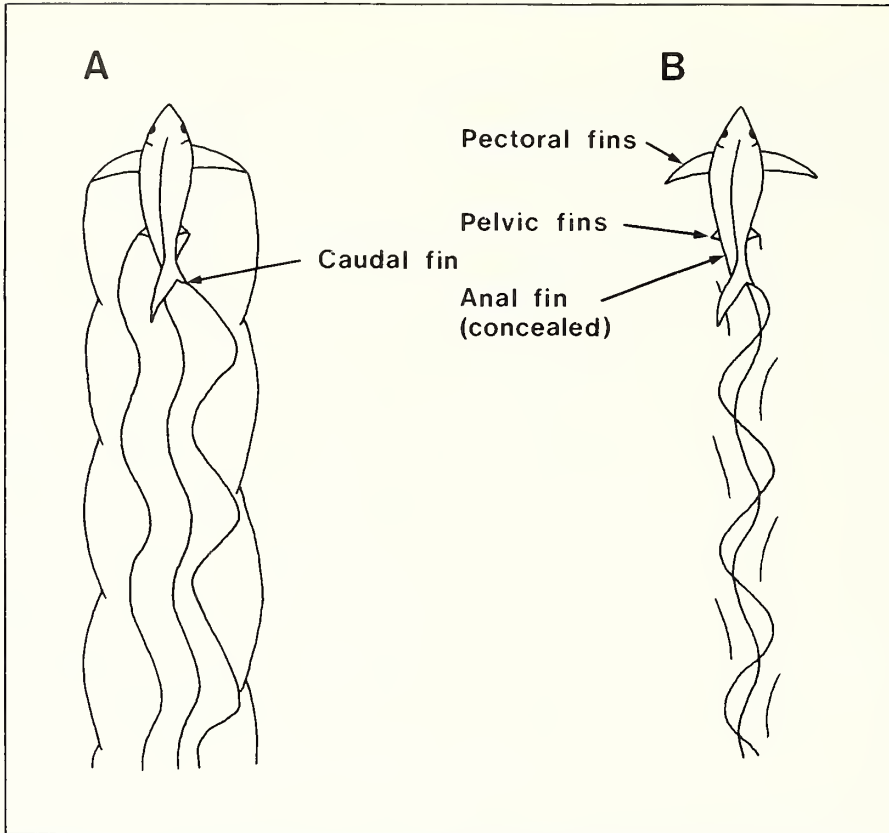
Description. The waves are of equal wavelength, but are out of phase, the phase difference ranging up to one half-cycle. One wave is of rather greater amplitude than the other. The larger ('outer') wave, whose lateral extremities are commonly faint, invariably cuts the smaller ('inner') wave. Rarely, an extra pair of discontinuous grooves is visible; these are sub-parallel to the inner wave, and lie one on each side of it, confined to the 'inside' of each bend (see fig. 1 of King 1965).

Comparison. There is more than one pair of continuous waves in *U. insolentia*. In *U. bina* the two waves are always parallel. *U. simplicitas* usually consists of an odd number of waves. *U. consulca* has an associated furrow.



TEXT-FIG. 2 (A, line drawing, and B, photograph). Rock slab E.3841, showing: E.3841a, *Undichna bina*; E.3841b, *U. britannica*, holotype; E.3841c, *U. consulca*, holotype; E.3841d, probable *U. consulca*. Note that, in specimen d, the only evidence for the sinusoidal grooves are the faint dimples bordering the right-hand side of the trail. The trails are in concave relief. From GR (2017 0751). Natural size.





TEXT-FIG. 3. Proposed correlation between fish fins and inscribed waves for: A, *Undichna simplicitas* (after Anderson (1976); note that the trail shown is a slightly asymmetrical one); B, *U. britannica*. See text for details.

Dimensions. Measurements (to the nearest 0.5 cm) of five representative Bude Formation specimens are as follows. The body-length calculation is discussed below.

	Wavelength (cm)	Amplitude of outer wave (cm)	Amplitude of inner wave (cm)	Phase difference (cm)	Calculated body length (cm)
E.3841b	16.0	6.5	3.0	2.0	26.0
E.3842a	13.0	4.0	2.5	1.5	16.0
Text-fig. 4, trail b	12.0	3.0	1.5	1.5	12.0
UR14404 ¹	14.0	3.0	2.0	2.0	12.0
Latex peel ²	42.0	12.0	4.5	2.5	48.0

¹ A line-drawing of this specimen is figured by King (1965, fig. 1), but his scale is incorrect, and should be one-third shorter.

² Taken from the type locality by Dr R. Goldring, and stored at the University of Reading.

Remarks. *U. britannica* was considered 'problematic' by Anderson (1976, p. 407), and illustrated under the caption "?*Undichna* sp." (her pl. 54, fig. 5); she opted to leave it unclassified, remarking on the uncertainty about its interpretation (i.e. fish versus mating crabs (see below)).

In all of the observed Bude Formation specimens, the two intertwined waves are only slightly out of phase. In contrast, the specimen illustrated by Anderson (1976, pl. 54, fig. 5) shows the two waves about 180° out of phase.

The overall trace is usually straight or gently curved, and extends for at least a metre or two (i.e. to the extremities of the exposure). In one case, a trace was observed to undergo a sudden sharp turn, doubling back on itself to make an angle of about 60°.

In the Bude Formation, *U. britannica* occurs in association (on the same parting surface) with *U. consulca* and *Kouphichnium* sp., the three types of trace cutting across one another (text-fig. 4). Any one parting surface typically shows five to ten *U. britannica* individuals per square metre.

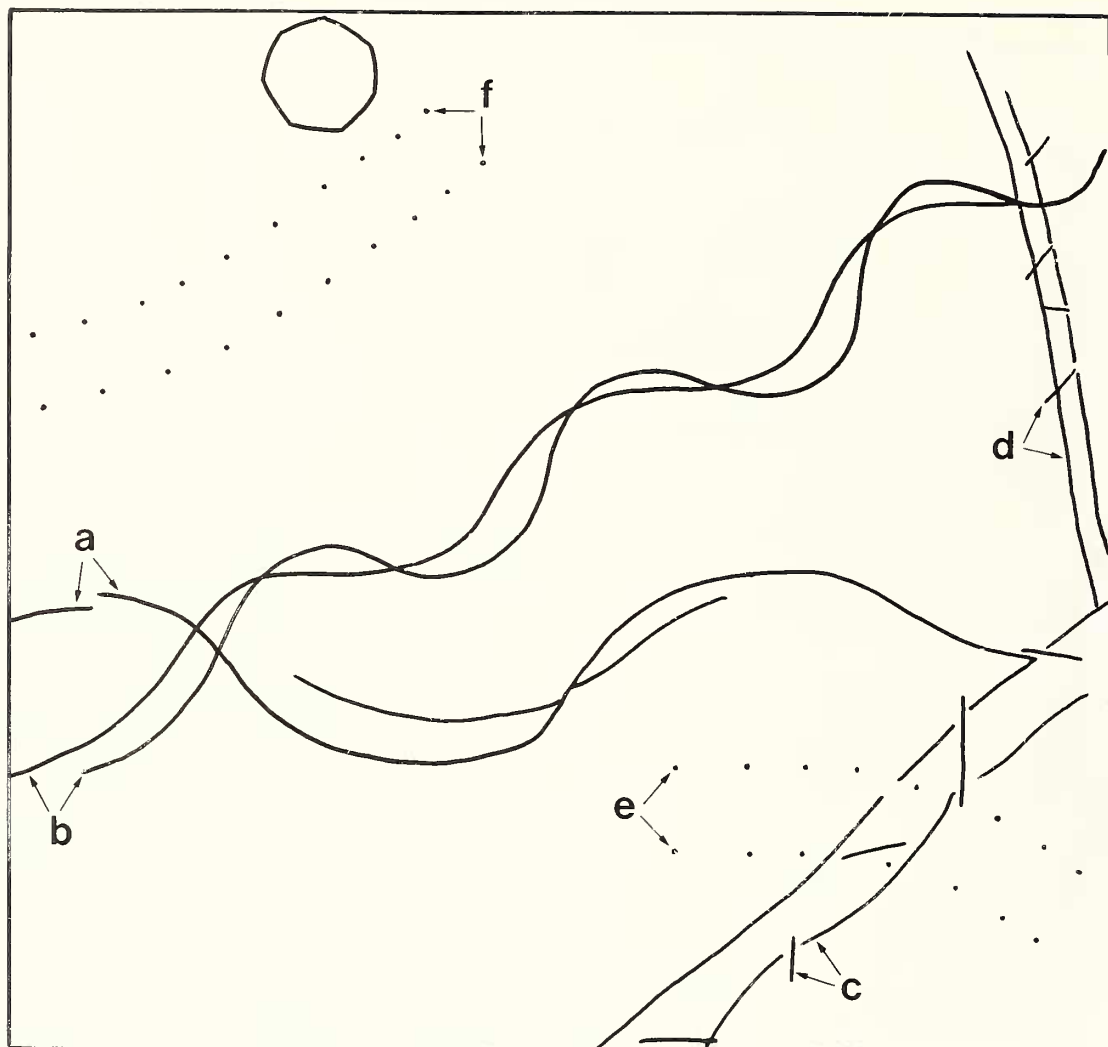
Interpretation. King (1965) argued that the out-of-phase sinusoidal waves here named *U. britannica* were formed by the dragging tails of a male–female pair of xiphosurids locked in a mobile ‘nuptial embrace’ (King 1965, fig. 1), with the male clinging to the back of the female as she walked toward the shoreline to lay her eggs. The implication is that the female for some reason walked a sinuous course. By way of a modern analogy, King cited Caster’s (1938) review of the behaviour of present-day king-crabs, which, during the mating season, habitually ‘seek the shore in pairs, the male often hanging onto the tail of the female’ (Caster 1938, p. 22). However, nowhere in his account does Caster indicate that the female walks a *sinuous* path during this seasonal migration. In fact, it seems most unlikely that the female, laden not only with her eggs but also with her mate, would follow anything other than a *straight* course. The fact that normal xiphosurid trackways (i.e. *Kouphichnium*) are straight to gently curved (e.g. text-figs. 4 and 8) indicates that there is no physiological reason why a xiphosurid should have followed a sinuous course. Hence, King’s mating-crab model is unsound, in that for a xiphosurid to meander would surely have been a waste of energy. A more logical explanation for the sinusoidal grooves is that they were produced by an organism, or part of an organism, which was biomechanically *compelled* to follow a sinuous course (e.g. the posterior fins of a fish). Two additional difficulties with King’s model are as follows:

1. The out-of-phase waves are never superimposed upon xiphosurid footprints (*Kouphichnium*). This is hard to reconcile with King’s proposal that the female crab was *walking* toward the shore. King ascribes the lack of footprints to the undertrack-fallout effect. However, this argument is unsatisfactory, since one would expect to see associated footprints in at least *some* cases, representing different undertrack levels.

2. The observation that the trails occasionally do a ‘U-turn’ (see above) is incompatible with King’s suggestion that the trails reflect a seasonal migration to the spawning ground.

It is submitted, therefore, that *U. britannica* is made not by xiphosurids, but by a fish swimming with its anal fin and caudal fin in contact with the substrate (text-fig. 3). The outer wave represents the caudal fin, since it cuts through (i.e. is ‘later’ than) the inner wave; its greater amplitude reflects the fact that the amplitude of undulation in a swimming fish increases posteriorly (Bainbridge 1962). Clearly, the anal and caudal fins of the fish in question must have projected lower than either (1) the pelvic fins, or (2) the pectoral fins, since the trail lacks any continuous, non-interfering wave pairs such as these paired fins would have produced (cf. text-fig. 3A). The discontinuous ‘side’ waves sometimes seen in *U. britannica* (text-fig. 3B) are thought to be due to the pelvic fins scratching the sediment briefly and alternately as the fish swam. An interesting parallel is found in Bainbridge’s (1962) laboratory observations of modern bream, dace, and goldfish: ‘during swimming a certain amount of rolling about the antero-posterior axis has been observed’ (Bainbridge 1962, p. 44). The rolling motion is ‘rather rarely observed’ and ‘seems most apparent during slower swimming’ (Bainbridge 1962, p. 45); this suggests that *U. britannica* specimens with and without ‘side’ waves are not necessarily the product of two different species of fish, but may instead be due to a single species which under certain circumstances swam with a slight roll.

It is possible to estimate the size of the fish responsible for *U. britannica* (cf. Anderson 1970). Bainbridge (1962) found, in his observations of modern fish, that the amplitude of the tail beat is approximately equal to one quarter of the body length; from this relationship comes the equation ‘Body length $\approx 4 \times$ caudal wave amplitude’. The table of dimensions given above includes an estimate of body length thus obtained. Assuming that Bainbridge’s relationship for modern fish is grossly applicable to the ancient, the fish responsible for *U. britannica* ranged in length between about 10 and 50 cm.



TEXT-FIG. 4 (A, line drawing, and B, photograph). Field view of a parting surface showing: a, b, *Undichna britannica*; c, d, *U. consulca*; e, f, *Kouphichnium* sp. The latter consists of pusher imprints and dragged-out walking-leg impressions (line drawing shows schematic pusher imprints only). Strata right way up, younging toward viewer. Note that various additional fragmentary specimens of *U. britannica* are visible. Cliff base at type locality of *U. britannica* and *U. consulca*, GR (2017 0751). Concave relief. $\times 0.5$.

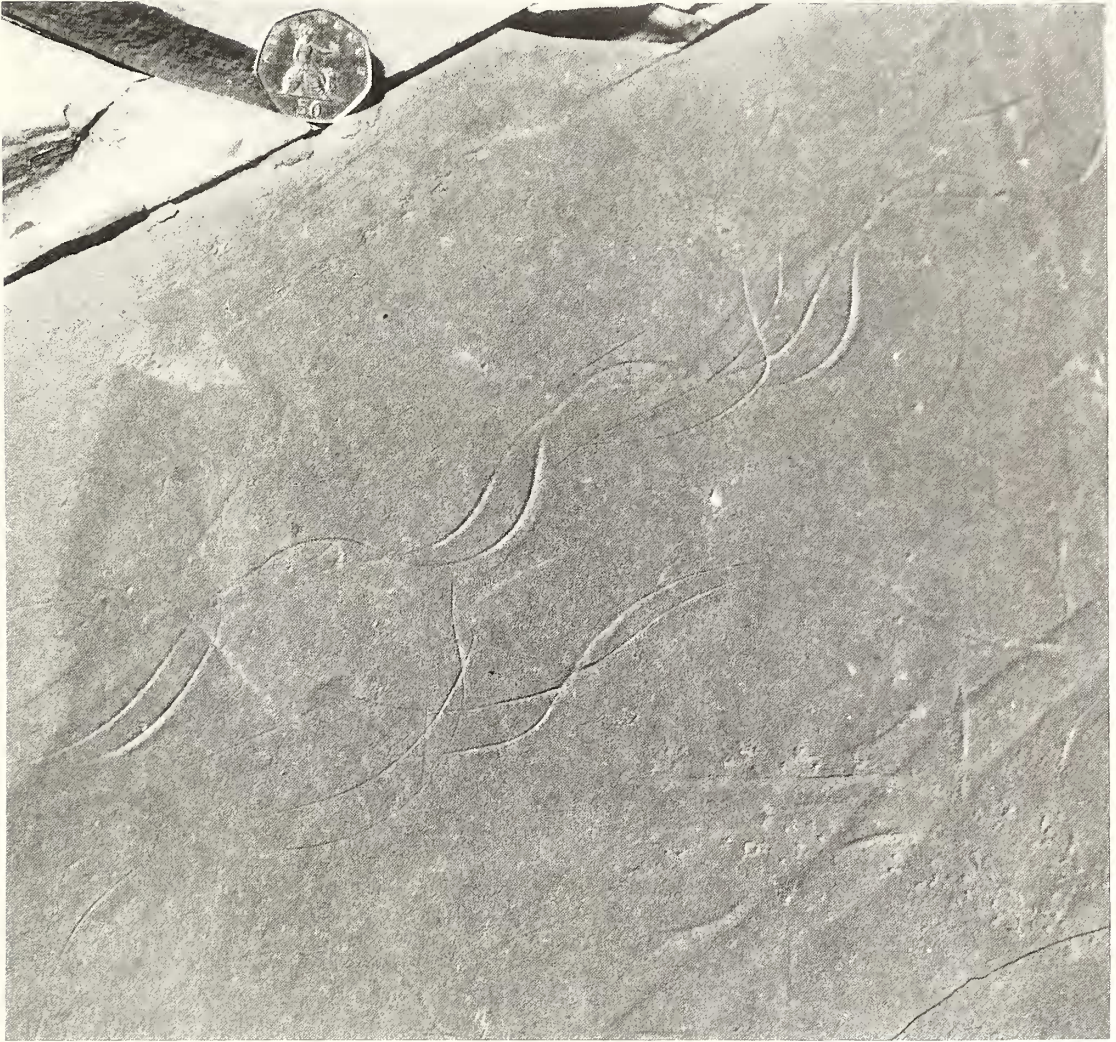
Undichna consulca nov. ichnosp.

Text-figs. 2, 4, 5

Derivation of name. Con (form of cum, Latin) = with; sulcus (Latin, from Greek) = a furrow.

Types. Holotype: specimen E.3841c, same horizon and locality as the *U. britannica* holotype. Paratypes: E.3841e, E.3843, both same horizon and locality as holotype; E.3838a, same horizon, cliff base at GR (2016 0895).

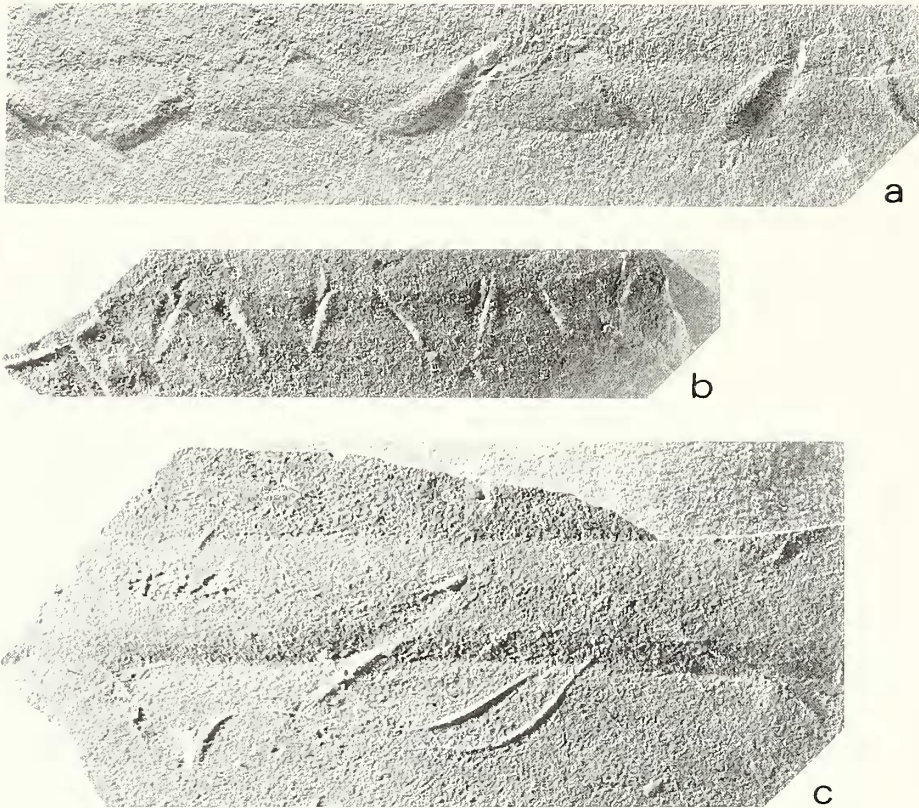
Diagnosis. A composite trace consisting of a simple, unornamented, very shallow furrow, upon which is superimposed, throughout its length, a pair of intertwined grooves, each groove having



the form of a sinusoidal or slightly asymmetrical sinusoidal wave. The grooves may be either sharp or blurred.

Description. The furrow is straight to gently curving over distances of dm to m. It is smoothly concave-upward in transverse profile, and is symmetrically flanked by an identical pair of subtle, sharp-crested ridges. The inner face of each ridge merges smoothly downward, with declining gradient, into the floor of the furrow. The outer face decreases gradually in angle of dip away from the furrow, merging smoothly with the adjacent undisturbed 'plain' within a distance of a few mm.

The grooves are of equal wavelength, slightly out of phase, and of slightly differing amplitude (cf. the intertwined grooves of *U. britannica*). The higher amplitude ('outer') wave invariably cuts the lower amplitude ('inner') wave. The grooves are sharply incised in some cases; in others, they have a blurred or 'washed out' appearance (text-figs. 2 (trail c) and 5A, B). In some specimens, the lateral extremities (i.e. the crests and troughs) of the sinusoidal waves are missing, so that the grooves are reduced to a series of paired 'flick marks' inclined in alternating directions down the length of the trail (text-figs. 4 and 5A, B). The amplitude of the outer wave exceeds



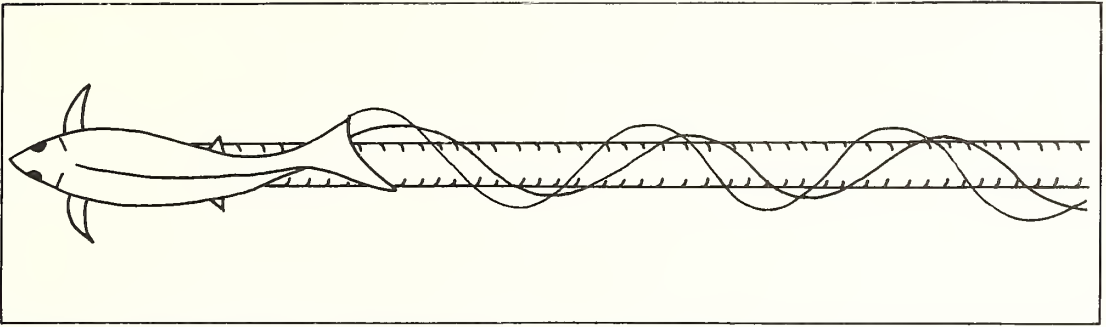
TEXT-FIG. 5. *Undichna consulca*, paratypes, natural size. *a*, undersurface of rock slab E.3841, showing *U. consulca* specimen E.3841e. Note that the lateral extremities of the (blurred) sinusoidal waves are missing. Convex relief. Locality as in text-fig. 2 (same slab). *b*, rock slab E.3838, showing specimen E.3838a. Part of a *Koupichnium* specimen (E.3838b) is also visible, at the extreme left, running bottom right to top left. Concave relief. From GR (2016 0895). *c*, undersurface of rock slab E.3843. Note that (i) the sinusoidal grooves are sharply incised; (ii) both grooves suddenly terminate toward the left, suggesting that the trail-maker abruptly stopped; and (iii) the grooves are 'off-centre' with respect to the furrow. Convex relief. Locality as in text-fig. 2.

the width of the furrow; the same is not always true of the inner wave. The waves may either straddle the furrow symmetrically, the outer wave overlapping both of the marginal ridges, or they may be displaced to one side, straddling one ridge but not the other (text-figs. 2 (trail c) and 5c).

Both the furrow and the waves must be present to allow positive identification as *U. consulca*.

Comparison. The furrow immediately distinguishes *U. consulca* from the other species of *Undichna*. Even if the grooves are missing or very faint, the furrow could not be confused with other gutter-like ichnogenera: *Gordia* forms complex looping patterns, and *Scolicia* is heavily ornamented. A shallow furrow occurs at the highest undertrack level of *Koupichnium*, but is accompanied by a blurred central (telson) groove (e.g. Goldring and Seilacher 1971, fig. 2).

Dimensions. The maximum depth of the furrow (i.e. the elevation difference between the base of the furrow and the crests of the flanking ridges) is 1 mm. The elevation of the ridges, relative to the adjacent 'plain', never exceeds



TEXT-FIG. 6. Proposed origin of *Undichna consulca*. The furrow is produced by the fish's belly dragging in the surficial mud, while the two sinusoidal grooves are inscribed by the fish's anal fin and caudal fin (cf. text-fig. 3B).

0.5 mm. Other dimensions, from seven representative specimens, are as follows (measurements to the nearest 0.5 cm, except furrow width):

	Wavelength (cm)	Amplitude of outer wave (cm)	Amplitude of inner wave (cm)	Width of furrow (mm)	Calculated body length (cm)
E.3841c	4.5	2.5	1.5	24	10.0
E.3841e	4.0	2.0	1.5	9	8.0
E.3843	7.0	2.0	1.5	18	8.0
E.3838a	2.0	1.5	1.5	7	6.0
E.3842b	5.0	2.0	1.5	16	8.0
UR14403	4.0	2.5	2.0	15	10.0
Latex peel ¹	5.5	2.5	?	12	10.0

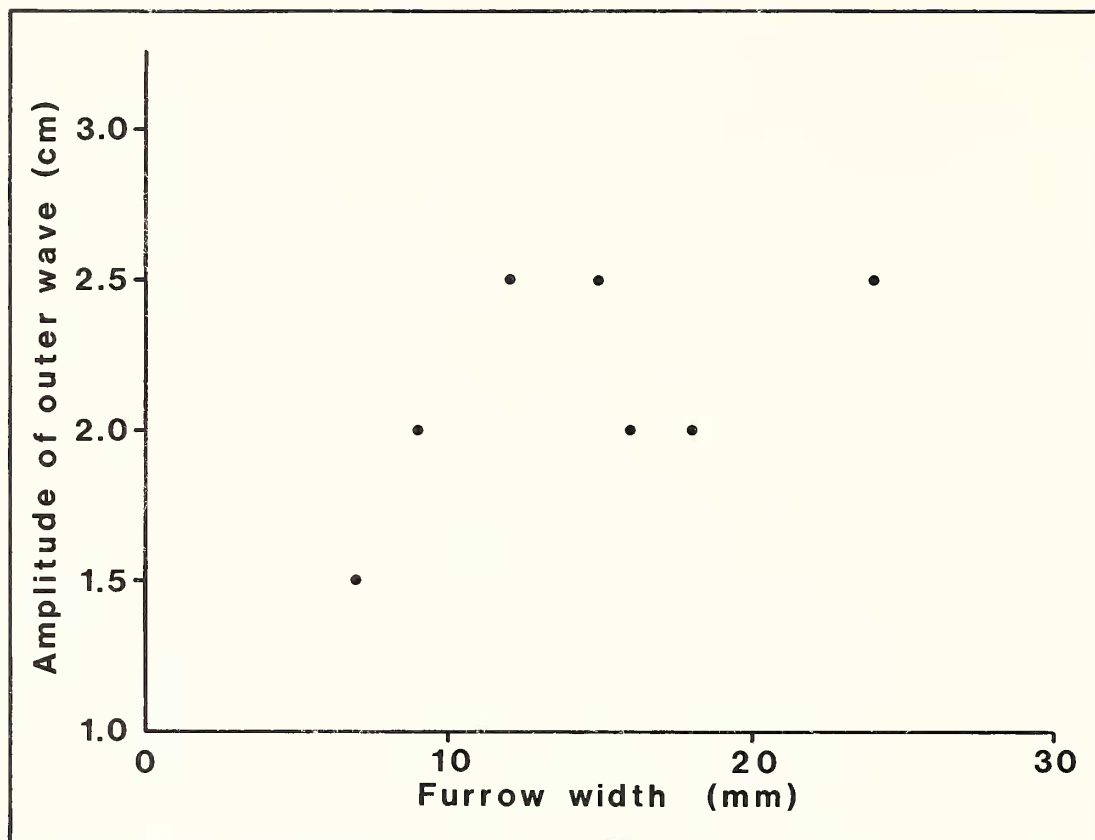
¹ Same peel as in table of dimensions for *U. britannica*.

Remarks. See the section on *U. britannica* for remarks about associated trace fossils. The density of *U. consulca* specimens on individual parting surfaces is typically between five and ten per square metre.

Interpretation. By analogy with *U. britannica*, the two sinusoidal grooves of *U. consulca* are interpreted as the drag marks of the caudal fin and anal fin of a fish swimming in contact with the substrate (text-fig. 6). Specimens in which the grooves are blurred are probably surface traces, as opposed to undertraces; this is because surface traces tend to be 'less distinct . . . because they often become blurred by collapse and water action' (Goldring and Seilacher 1971, p. 428). Where the lateral extremities of the waves are missing, the possible explanations are: (1) they were not formed, perhaps because the fish swept its tail slightly upward at the end of each tail beat; or (2) they collapsed or were washed out.

An important question is whether the furrow and the sinusoidal grooves were formed simultaneously by a single animal (i.e. a fish), or whether the grooves were formed significantly later by a fish which was following a pre-existing furrow in the hope of finding (and eating?) the furrow-maker. The second of these two alternatives is highly unlikely, because (1) furrows are *always* accompanied by grooves, and (2) there is a definite correlation between furrow width and groove dimensions (text-fig. 7).

Considering the anatomy of a fish, the furrow is thought to represent the impression of a fish's belly dragging through the uppermost millimetre or two of the surficial sediment (text-fig. 6). Material displaced sideways by the fish was heaped up to form the low ridges marginal to the furrow. The furrow was then overprinted by the sinusoidal grooves, representing the drag marks of the anal fin and the caudal fin. The fact that the supposed belly impression is not sinusoidal reflects the fact that the



TEXT-FIG. 7. Plot of furrow width versus (outer) groove amplitude for seven representative specimens of *Undichna consulca* (see table of dimensions in text). Note the positive correlation. A better correlation might have been obtained but for the fact that (1) the amplitude values were only measured to the nearest 0.5 cm, and (2) the furrow width of individual specimens varies slightly, depending on the undertrack level sampled (see text).

amplitude of undulation in a swimming fish decreases anteriorly, reaching zero (or almost zero) near the back of the head (Bainbridge 1962). Those specimens of *U. consulca* in which the grooves are off-centre with respect to the furrow are possibly due to a fish swimming across a current.

Examples of *U. consulca* on modern sea- or lake-floors appear to be unknown. The nearest morphological analogue may be the 'snout-marks' illustrated by Stanley (1971, fig. 4), consisting of slightly curving leveed furrows formed by fish feeding in a snout-down posture. Unlike *U. consulca*, however, these modern furrows appear to be relatively short (cm-dm), and there is no sign of any sinusoidal grooves. These modern traces are formed by fish rooting for food in the mud (Stanley 1971; Marshall and Bourne 1964); in contrast, the *U. consulca* fish is thought to have been coasting along the bottom in search of epifaunal prey.

The body length of the *U. consulca* fish, based on the caudal-wave amplitude (see the section on *U. britannica*, and the table of dimensions for *U. consulca*), ranged from 5 to 10 cm.

Given the similarity between *U. britannica* on the one hand, and the sinusoidal grooves of *U. consulca* on the other, the question arises whether the former is simply the undertrail of the latter. This is thought unlikely, because the measurements presented in the tables above suggest that the *U. britannica* fish was substantially larger than the *U. consulca* fish (note that the measured specimens were selected at random).

With regard to the 'fallout sequence' in *U. consulca*, there appear to be two separate cases: (1) in specimens in which the grooves are symmetrically disposed over the furrow (e.g. text-fig. 5A, B), the grooves presumably fall out last, since they incise even the deepest part of the furrow; (2) in the remaining specimens, whose grooves are asymmetrically disposed, the furrow and the grooves appear to fall out at approximately the same level (e.g. text-fig. 2, trail d), suggesting that the fish swam in a more 'tail-up' attitude in such cases.

Undichna simplicitas Anderson, 1976

Text-fig. 8

Description. In its most complete form, *U. simplicitas* consists of one (inner) pair of parallel sinusoidal waves, one (outer) pair of non-parallel scolloped waves, and a single unpaired wave (text-fig. 3A). However, it is not uncommon to find the unpaired wave alone (Anderson 1976). Solitary unpaired waves occur in the Bude Formation (text-fig. 8), and are accordingly assigned to *U. simplicitas*.

Interpretation. The unpaired wave of *U. simplicitas* was probably formed by one or the other of two unpaired fins which most fish carry on their undersides, namely the anal fin or the caudal fin. Anderson (1976) favoured the caudal fin, for unspecified reasons (text-fig. 3A). Where only a solitary wave is encountered, it is reasonable to infer that either the anal fin or the caudal fin protruded lower than any other part of the body. It is impossible to say *which* fin, anal or caudal, was responsible, because the anal fin is the lowest in some genera, while the caudal fin is the lowest in others (see the many fish restorations in Traquair (1877–1914), Woodward (1891), Romer (1966), and Miles (1971)).

A case could be made for erecting a separate new ichnospecies to accommodate all occurrences of unpaired waves, for two reasons. First, solitary waves are morphologically very different from 'complete' specimens of *U. simplicitas*. Secondly, in assigning solitary waves to *U. simplicitas*, Anderson is implying that such a wave represents the undertrail of a more complete specimen of *U. simplicitas*; in other words, it was produced by the same type of fish; however, this is an unreasonable assumption, since an unpaired wave could equally likely be the undertrail of *U. britannica* or *U. consulca*; alternatively, the solitary wave may not be an undertrail at all. Before any new ichnospecies is erected, however, a restudy of Anderson's (1970, 1976) material should be undertaken, in order to (1) define the full range of variability in the unpaired waves, and (2) nominate type specimens.

THE IDENTITY OF THE TRACE MAKERS

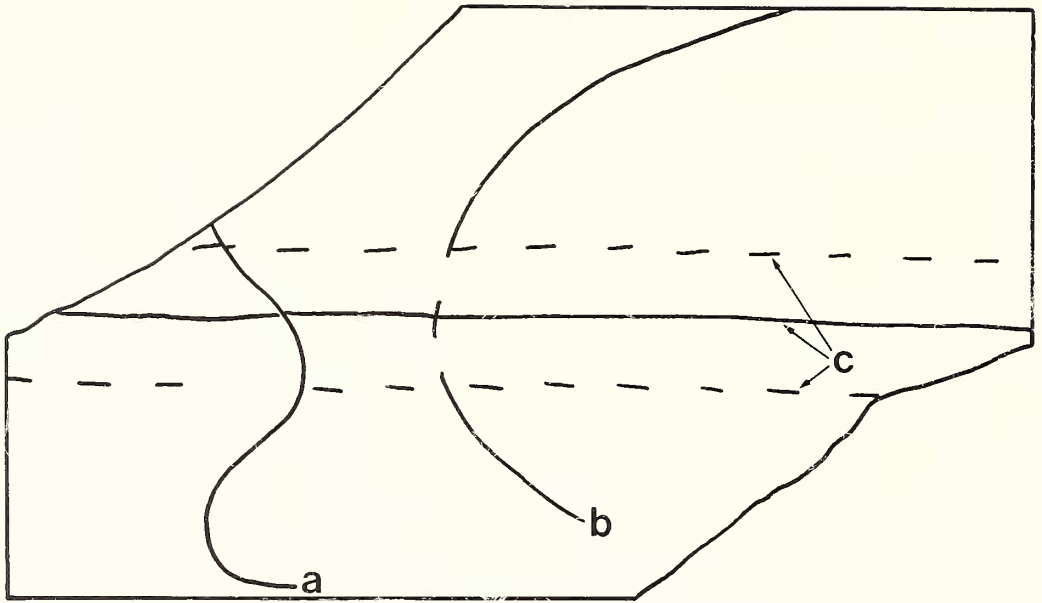
The purpose of this section is to identify which, if any, of the four species of fossil fish discovered in the Bude Formation could have made the four types of fish trail described above. The four fish are: *Acanthodes wardi* (Woodward 1891, Part 2, fig. 1), *Cornuboniscus budensis* (text-fig. 9), *Elonichthys aitkeni* (Traquair 1877–1914, pl. 16), and *Rhabdoderma elegans* (Forey 1981, text-fig. 9).

U. bina

As mentioned earlier, the parallel sinusoidal waves of *U. bina* were probably made by a fish whose pelvic fin-tips were lower than any of the other fin-tips. This condition is not satisfied by any of the above fish, with the possible exception of *E. aitkeni*. (Unfortunately, the two specimens of *E. aitkeni* illustrated by Traquair, including the type specimen, are contorted, and the fin relationships are therefore not visible.) If *E. aitkeni* is *not* responsible for *U. bina*, then some other chondrosteian fish could be responsible, since this group includes many genera with 'low' pelvic fins. Alternatively, among the other six groups of Upper Carboniferous fishes (Miles 1971), certain crossopterygians, dipnoans, elasmobranchs, and holocephalans are likewise of suitable morphology to have produced *U. bina*.

U. britannica

If the intertwined grooves of *U. britannica* were produced by the anal and caudal fins of a fish, as inferred earlier, then the fish must have swam with its anal and caudal fin-tips lower than any other



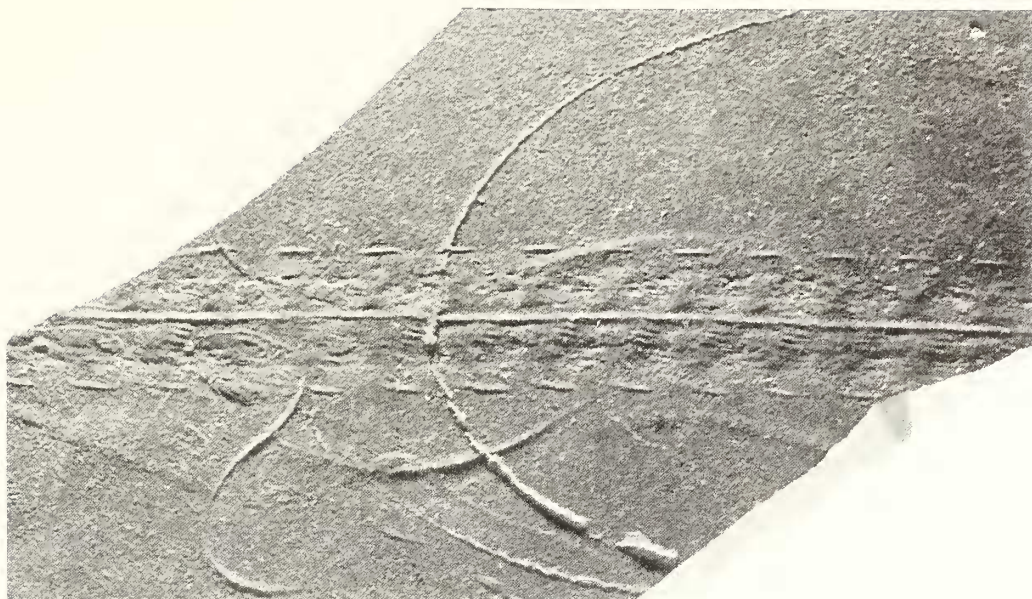
TEXT-FIG. 8 (A, line drawing, and B, photograph). Rock slab E.3837, showing: E.3837a, *U. simplicitas*; E.3837b, possible *U. simplicitas*; E.3837c, *Kouphichnium* sp. The latter consists of the following elements: (i) an outer set of regularly spaced genal-spine impressions; (ii) a central telson groove; and (iii) blurred walking-leg and pusher imprints. This *Kouphichnium* specimen represents a shallower undertrack level than trails e and f in text-fig. 4 (see text). Convex relief. From GR (2017 0751). Natural size.

fin-tips. The pelvic fins, responsible for the discontinuous 'side' grooves, evidently did not extend so far. Based on these characteristics, neither *A. wardi* nor *R. elegans* could have produced *U. britannica*. The morphology of *C. budensis* seems to be approximately correct (text-fig. 9); however, the largest of twenty-five specimens examined by White (1939) is only 7 cm long (allowing for its missing tail), substantially shorter than the 10–50 cm fish inferred from the measurements of *U. britannica*. Finally, the morphological suitability of *E. aitkeni* is unknown, due to the imperfect condition of the type specimen; however, this fish may also have been too small, the maximum length being about 18 cm according to Woodward (1891).

It seems likely, therefore, that *U. britannica* was made by a fish whose fossilized remains have yet to be found in the Bude Formation. Based on the morphology deduced above, only one of the seven groups of Carboniferous fishes, namely the chondrosteans, includes suitably shaped genera. However, few chondrosteans exceed 20 cm in length. One genus which is of the correct morphology and size for *U. britannica* is *Acrolepis* (e.g. Traquair 1877–1914, pl. 25, fig. 7). Specimens of *Acrolepis* examined by Traquair range from 9 cm (excluding the missing head) to 65 cm. *Acrolepis* is also of the correct age, ranging from Lower Carboniferous to Upper Permian (Romer 1966). The possibility exists, therefore, that *Acrolepis* will one day be discovered in the Bude Formation.

U. consulca

The furrow and the intertwined grooves of *U. consulca* permit the following deductions concerning the morphology of the fish responsible: (1) the anal and caudal fins (responsible for the grooves) must have protruded lower than the fish's belly (responsible for the furrow), since the grooves are incised into the furrow; (2) the absence of any 'paired and parallel' waves attributable to the pelvic fins implies that these fins were high enough to remain clear of the sediment; and (3) the pectoral fins must have



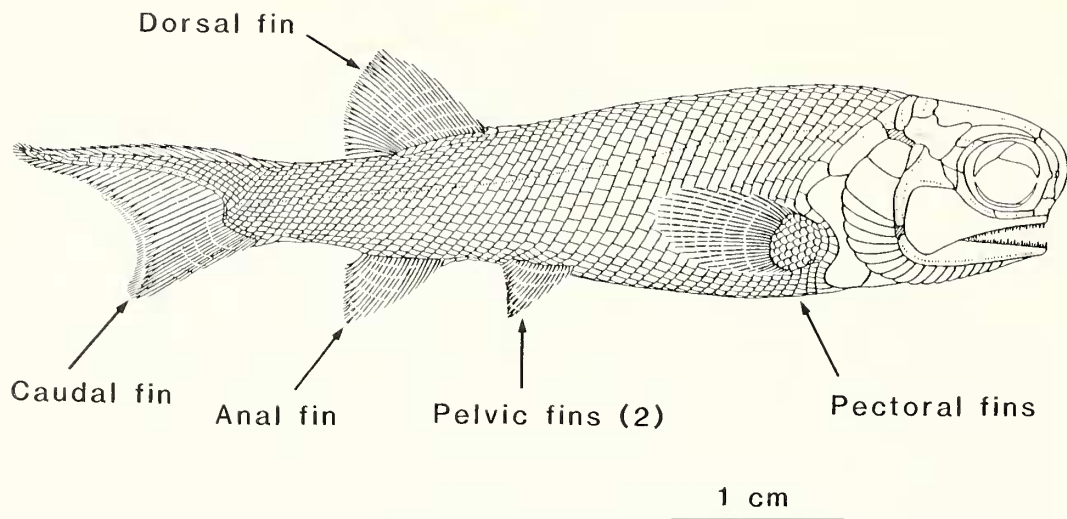
been inserted high up the flank of the body, otherwise they would have fouled the bottom whenever the fish's belly was touching the sediment.

The last of these anatomical deductions provides an important clue to the identity of the fish in question. One of the fossil fish in the Bude Formation, *C. budensis*, is characterized by very unusual pectoral fins, mounted high on the body (text-fig. 9); in fact, the pectorals are so unusual that White (1939) erected a new genus, of which *C. budensis* is the only known species; furthermore, this fish is unknown outside the Bude Formation. White (1939, p. 52) remarked that 'the most striking feature of this little fish is the form of the pectoral fin': unlike normal palaeoniscoid (suborder) fishes, in which the pectoral fins were inserted low down the flank and held more-or-less horizontally (White 1939; Westoll 1944), the pectorals of *C. budensis* are inserted vertically, high up the flank (text-fig. 9). Normal palaeoniscoids, therefore, would have been unable to engage in 'belly-skimming' without dragging their pectoral fins; in contrast, the pectorals of *C. budensis* would have been well clear of the sediment.

Westoll (1944) argued that White's reconstruction of the pectoral fins of *C. budensis* (as in text-fig. 9) is incorrect, since if held vertically instead of horizontally, the pectorals could not have fulfilled their usual role of acting as hydrofoils to counterbalance the tail-lift induced by the heterocercal tail. However, Westoll was neglecting the possibility of a belly-skimming mode of feeding, in which hydrofoil-type pectorals might actually be disadvantageous.

With regard to other morphological features of *C. budensis*, the anal and caudal fin-tips were suitably positioned to have produced the intertwined grooves of *U. consulca* (text-fig. 9). However, there is a potential difficulty with the pelvic fins: in the position shown (text-fig. 9), they would inevitably have dragged if the anal fin, caudal fin, and belly were in contact with the sediment, yet there is no record of this in *U. consulca*. The solution to the problem may be that the pelvic fins actually protruded *outward* more than is shown in White's reconstruction; indeed, Westoll (1944, p. 85) stated that 'Probably the drooping position in which they (the pelvic fins) are customarily restored in palaeoniscids (family) is misleading' (bracketed words added). Furthermore, the pelvic fins of *C. budensis* 'are placed well to the rear' (White 1939, p. 43); in this position, the pelvics are less likely to have contacted the sediment than are those of normal palaeoniscoids.

As well as having the correct morphology, *C. budensis* is the correct *size* to have produced *U. consulca*. The range in length of 4–7 cm for the twenty-five *C. budensis* specimens examined by White



TEXT-FIG. 9. Restoration of the external skeleton of *Cornuboniscus budensis*. After White (1939).

(1939) (allowing for incomplete specimens) compares favourably with the range of 5–10 cm calculated above from the dimensions of *U. consulca*. Moreover, *C. budensis* has been found in close stratigraphic proximity to *U. consulca*: the fish occurs only in the Saturday's Pit Shale (Freshney *et al.* 1979), which lies just 4 m above the *U. consulca*-bearing unit at the type locality.

Hence, there is a considerable body of evidence to suggest that *C. budensis*, or an undiscovered close relative, is the *U. consulca* fish. This conclusion is strengthened by the fact that no other known Upper Carboniferous fish had a suitable morphology.

It is interesting to speculate on what the belly-skimming fish's diet might have been. The fact that the furrow of *U. consulca* is flanked by ridges suggests that the fish was pushing the mud aside, rather than filtering it to extract contained invertebrates or plant detritus. Two additional factors militate against the idea that the food was contained in the mud: (1) there are no burrows in F2, suggesting that the mud lacked an infauna; and (2) *C. budensis* is unlikely to have favoured plant detritus, since it has sharp, conical teeth and a wide gape, suggesting a carnivorous diet. The evidence suggests that the fish was preying on live epifaunal organisms; of these, the only indication consists of xiphosurid trackways (*Kouphichnium*). The trackways are only 1 to 3 cm across; hence the xiphosurids might have been small enough for the (5–10 cm) fish to tackle.

U. simplicitas

It was suggested above that the solitary wave, here assigned to *U. simplicitas*, was produced by a fish whose caudal fin or anal fin extended lower than any other part of the body. Therefore, of the four fish species discovered in the Bude Formation, *A. wardi* and *R. elegans* can be discounted. The correct morphology is shown by *C. budensis*, but this fish was less than 10 cm long, and therefore could only have produced the smaller of the two *U. simplicitas* specimens visible in text-fig. 8. (Applying the body-length calculation discussed earlier, the amplitude of the larger trace (min. 5 cm) suggests a fish at least 20 cm long.) Whether or not *E. aitkeni* could have produced an unpaired wave is uncertain, owing to the poor condition of the type specimen (Traquair 1877–1914).

Acrolepis, proposed earlier as the likely maker of *U. britannica*, is of suitable shape and size to have produced the larger of the two *U. simplicitas* specimens. Thus, *Acrolepis* may have been responsible for both (the larger) *U. simplicitas* and for *U. britannica*; this is consistent with the idea, advanced earlier, that solitary-wave specimens of *U. simplicitas* could, in some cases, represent the undertrail of *U. britannica*. Similarly, the deduction that *C. budensis* could be responsible for both (the smaller) *U.*

simplicitas and for *U. consulca* is consistent with the idea that the former is potentially the undertrail of the latter.

Absence of trails corresponding to two of the Bude Formation fish

From the foregoing discussion, it is apparent that *A. wardi* and *R. elegans* (and possibly *E. aitkeni*) cannot be matched to any of the four types of trail described here. In the case of *A. wardi*, the lack of corresponding trails is not surprising, since acanthodians were probably mid- to surface-water feeders throughout their history (Miles 1971). *R. elegans*, which is a coelacanth, may or may not have swum in contact with the bottom; however, any trails which it happened to produce might be other than sinuous, since the modern coelacanth (*Latimeria*) appears to scull with its paired fins instead of waving its tail (Mackenzie 1987).

Salinity preference of Bude Formation fish

It has been shown that *C. budensis* was probably the maker of *U. consulca*. This suggests that *C. budensis* was tolerant of both brackish- and fresh water, since the fish and its trails have been found in brackish facies (F1) and in fresh facies (F2) (respectively; see Introduction).

Evolution of endemic fishes in Lake Bude

As discussed earlier, *C. budensis* appears to have evolved special features to facilitate a belly-skimming mode of life. The fact that this fish has never been found outside the Bude Formation suggests that it may have been endemic to Lake Bude. Analogous circumstances are found in *modern* lakes, where reproductive isolation is common (e.g. Beadle 1981), giving rise to endemic fishes that are specialized to take advantage of the local conditions.

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ROGER HIGGS

Department of Earth Sciences
University of Oxford
Parks Road, Oxford
OX1 3PR, UK

Present address:

Geological Survey of Canada
Pacific Geoscience Centre
9860 West Saanich Road
Sidney, B.C. V8L 4B2
Canada

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Note added in proof

With regard to the section on p. 271 entitled 'Absence of trails . . .', a paper by Fricke *et al.* on locomotion of the modern coelacanth (*Latimeria*) appeared in 1987 (*Nature*, **329**, 331–333). These authors observed *Latimeria* frequently resting, but not swimming, in contact with the bottom. Assuming that ancient coelacanths, including *R. elegans*, behaved similarly, they are unlikely to have produced trails.